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Multievent capture-recapture analysis reveals individual foraging specialisation in a generalist species

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*Running Head:* Foraging specialisation in generalist storks

ABSTRACT. Populations of species typically considered trophic generalists may include specialised individuals consistently feeding on certain resources. Optimal foraging theory states that individuals should feed on those resources most valuable to them. This, however, may vary according to individual differences in detecting or processing resources, different optimization criteria, and competitive abilities. White storks (*Ciconia ciconia*) are trophic generalists at the population level. Their European population recovery has been attributed to increased wintering in Southern Europe (rather than Africa) where they feed upon new anthropogenic food subsidies: predictable dumps and less predictable and more difficult to detect but abundant invasive *Procambarus clarkii* crayfishes in ricefields. We studied the foraging strategies of resident and wintering storks in SW Spain in ricefields and dumps, predicting that more experience in the study area (residents vs. immigrants, old vs. young) would increase ricefield specialisation. We developed the first multievent capture-recapture model to evaluate behavioural consistency, analysing 3,042 observations of 1,684 banded storks. There were more specialists among residents (72%) than immigrants (40%). All resident specialists foraged in ricefields, and ricefield use increased with individual age. On the other hand, immigrants specialised on either dumps (24%) or ricefields (16%) but the majority were generalists (60%). Our results provide empirical evidence of high individual foraging consistency within a generalist species and a differential resource selection by individuals of different ages and origins probably related to their previous experience in the foraging area. Thus, future changes in food resource availability at either of the two anthropogenic subsidies (ricefields or dumps) may differentially impact individuals of different ages and origins making up the wintering population. The use of multievent capture-recapture modelling has proven useful for studying inter-individual variability in behaviour.

**Keywords:** ecological processes, anthropogenic food subsidies, niche specialisation, foraging behaviour, White stork, *Ciconia ciconia*, multievent.

## INTRODUCTION

A large number of animal species benefit from anthropogenic food subsidies (e.g. refuse dumps, fishery discards or feeding stations) where high amounts of food are highly predictable in space and time (Oro et al. 2013). Anthropogenic food subsidies have promoted life history changes in many species, causing increases in their populations and even cascading effects in food webs and ecosystems (Robb et al. 2008, Carey et al. 2012, Cortés-Avizanda et al. 2012). However, little is known about individual consistency in the use (or lack of use) of food subsidies, or about the causes behind this individual specialisation (Oro et al. 2013). This is relevant because food subsidies affect the body condition, reproduction, home range, spatial distribution, and survival of individuals (Oro et al. 2013). For instance, Annett and Pierotti (1999) reported that Western gulls (*Larus occidentalis*) strongly relying on human refuse had lower life-time reproductive success than individuals feeding on natural resources (i.e., fish), and suggested that individual differences in resource use may be heritable. Moreover, individuals using food subsidies may be a non-random subset of the population (e.g., weaker individuals, Votier et al. 2010). Thus, not only the proportion of the population using food subsidies, but also the individual traits associated with their use would predict the impact of food subsidies upon population dynamics. Particularly, the consequences of a drastic reduction of food subsidies would greatly differ if it affects the most successful breeders vs. the weakest individuals of the population.



This problem is thus framed within the wider topic of individual specialisation, which is gaining momentum after the first review on the subject by Bolnick et al. (2003) in which they noted that “most empirical and theoretical studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent. This simplification is only justified if interindividual niche variation is rare, weak, or has a trivial effect on ecological processes”. Their review challenged this “rare interindividual niche variation” by reporting a strong and widespread occurrence of individual resource specialisation in different taxa, and their individual and population consequences. A recent review (motivated by a sudden increase in studies on individual specialisation) confirmed these conclusions (Araújo et al. 2011). While it was recognized that the current early development of the topic does not allow for strong hypotheses on the factors governing resource specialisation in a given population, foraging theory was highlighted as a candidate framework (Araújo et al. 2011).

Optimal foraging theory states that individuals feed on those resources most valuable to them, according to the diversity and abundance of resources and on individual traits (Araújo et al. 2011). Three non-exclusive mechanisms have been proposed to explain the relationship between optimal foraging and individual traits (Araújo et al. 2011). First, phenotypic variation among individuals may change optimal diets according to individual ability to detect or process different resources resulting in divergent rank preferences. Second, individuals may present different optimal diets due to different physiological requirements (e.g., specific nutrients for reproduction) or may differ in their optimization criteria (e.g., some prioritizing safety regarding predation risk while others prioritizing energy intake). Third, individuals may have the same optimal diets but different competitive abilities (e.g. dominant individuals may displace subordinate individuals

from the optimal resources).

The white stork (*Ciconia ciconia*) is a good candidate species as a model for assessing individual foraging strategies on anthropogenic food subsidies. This large-sized migratory wading bird preys on a wide range of animals, including insects, fish, amphibians, reptiles, small mammals and birds, but also makes use of waste resources. European populations of the species suffered a drastic decline after 1945 related to long drought periods in African wintering grounds, habitat deterioration, and casualties from power lines along their migration routes (Kanyamibwa et al. 1990, Barbraud et al. 1999, Schaub et al. 2005). Spanish stork populations have become sedentary since the 1980s, and northern European populations shortened their migration distances to overwinter in Spain. Currently, ca. 4,000 storks are wintering in southwest Spain (Doñana marshlands), including individuals of different origins: local residents and immigrant individuals from Germany, France, Netherlands and Switzerland (Aguirre 2013). This migratory behavioural change was related to the increase in food availability (mainly in refuse dumps) in Spain in recent decades (Tortosa et al. 2002, Rendón et al. 2008, Ramo et al 2013). Moreover, access to predictable and abundant food at dumps contributed to the concentration of breeding distribution, an increase in breeding success and juvenile survival, and to the advancement of the recruitment age of white storks (Tortosa et al. 2002). Contemporaneous with the increase in food availability at dumps, the introduction and rapid spread of the exotic invasive red swamp crayfish (*Procambarus clarkii*) in the Doñana marshlands contributed to the substantial increase of the white stork local breeding and wintering population (Rendón et al. 2008, Tablado et al. 2010).

The red swamp crayfish is a species native to the southeastern United States and northern Mexico that colonized the study area in 1973 and has increased in numbers since then, becoming

an important food subsidy for the community of predators in the area (Tablado et al. 2010). Storks breeding in the area intensely feed on crayfish during the breeding season (Tablado et al. 2010), feeding their nestlings with this abundant food resource (Negro et al. 2000). However, during winter, feeding in dumps may be easier than feeding on crayfish in ricefields (Correia and Ferreira 1995). Dumps are easy to locate at a distance and provide a large food supply predictable in space and time (Oro et al. 2013). Crayfish in ricefields, however, require more advanced skills to locate and prey upon than organic rubbish at dumps. During the wintering season, crayfish are only easily available after the ploughing of ricefields by farmers. Consequently, storks have to either relate the activity of farmers to the ephemeral availability of easier-to-capture crayfish or rely on public social information to locate this prey.

Currently, refuse at dumps and crayfishes from ricefields are the main food resources for wintering (either resident or immigrant) white storks in southern Spain (Tortosa et al. 1995, Tablado et al. 2010). Habitat changes or the occurrence of new food sources may provide new opportunities for ecological/evolutionary changes in the species, but anthropogenic food subsidies may also lead to ecological traps affecting the populations permanently (Oro et al. 2013). Moreover, if resident and immigrant individuals differ in their level of specialisation on the two main food resources, any changes in the resource availability at a local level may have different consequences for birds of different origins. Thus, describing potential individual specialisation and understanding their causes within this species is important both from a theoretical and an applied perspective.

This scenario represents a valuable opportunity to study the occurrence of inter-individual differences in the use of food subsidies (i.e., specialisation on crayfishes or rubbish) in relation to

individual traits. We hypothesized that foraging patterns differ between resident and immigrant individuals and with age. White storks exhibit very high annual nest-site fidelity (87%, Barbraud et al. 1999) and breeding dispersal distances are generally short ( $18 \pm 41$  Km) (Itonaga et al. 2010); thus, old residents should have better knowledge of the area than immigrants and young birds. Moreover, resident storks are known to consume high amounts of crayfish during the breeding season in the study area (Tablado et al. 2010), suggesting a high nutritional value of this prey (Negro et al. 2000). However, crayfishes are not usually found in the stork diet outside the study area (Negro et al. 2000), and thus immigrants may be unfamiliar with this food resource and more familiar with rubbish consumption given that dumps are present throughout the species breeding range. Consequently, in agreement with the hypothesis of inter-individual phenotypic/genetic differences related to individual ability to detect particular food resources (hypothesis 1 in Araújo et al. 2011), residents may present greater abilities to detect and consume crayfishes. On the other hand, while food availability in refuse dumps is highly predictable in space and time, red swamp crayfishes remain buried under mud during the autumn-winter (Correia and Ferreira 1995), becoming available when ricefields are ploughed (also during autumn-winter), thus being less predictable. Again, due to their greater experience in the area, residents and older individuals may consume crayfishes in higher proportions (hypothesis 1 in Araújo et al. 2011). On the contrary, during the wintering (i.e., non-breeding) season no differences in physiological requirements between individuals are expected (hypothesis 2 in Araújo et al. 2011). Similarly, competitive exclusion (hypothesis 3 in Araújo et al. 2011) is not expected as both crayfishes and rubbish are widely available at the Doñana wintering area and defense of food for a single stork is difficult; in fact, storks typically forage in loose groups where aggressive interactions are rare (authors' own

data).

We tested the existence of divergent individual foraging preferences (hypothesis 1 in Araújo et al. 2011) in relation to residence status and age by studying individual foraging strategies (either generalism or specialisation) of banded resident and immigrant white storks in their main European wintering area (Doñana marshes, SW Spain, Aguirre 2013). We used state-of-the-art capture-recapture modelling, developing specific multievent finite-mixture models originally used to account for capture heterogeneity (Pledger 2000, Pradel 2005). Models evaluated the extent of individual foraging specialisation on the available anthropogenic food subsidies (rubbish at dumps and crayfishes in ricefields) and quantified resource utilisation as a function of residency status (taking into account residency uncertainty for some individuals) and individual age.

## METHODS

**Field work** —From October 1st to December 19th 2003, two observers travelled through the white stork's main wintering area in SW Spain, which covers ca. 10,000 Km<sup>2</sup> (Fig. 1), looking for foraging individuals. The study area includes seven dumps surrounding a vast surface area (43,905 ha) of marshlands transformed for rice crops since 1931 in the area of Doñana National Park (Ramo et al. 2013). Travelling via unpaved roads crossing the marshlands allowed the monitoring of a number of unploughed ricefields as well as to locate a total of 17 ricefield localities (Fig. 1) asynchronously ploughed during the study period where red swamp crayfishes were made available for storks during several days after ploughing (Appendix A). Therefore, crayfishes were available at some ricefields throughout the study period, varying temporarily in their spatial location. Due to permit constraints, visits to dumps were periodic, ca. once a week. In



total, we recorded foraging storks during 106 visits to ploughed ricefields and 48 visits to the dumps (see Appendix A for more field work details).

**Individual data**—During the study period (lasting 80 days) dumps and ricefields were sampled on 35 and 42 different days, respectively (Appendix A). A total of 3,042 bands were identified and georeferenced, belonging to 1,684 different individuals. Thanks to a long-lasting banding program and several concurrent studies (Jovani and Tella 2004, 2007, Blas et al. 2007, Baos et al. 2012), many white storks were known to breed (or live) in the study area during the previous two breeding seasons. In particular, 876 nests in 2002 and 1,056 nests in 2003 were monitored, identifying a total of 535 resident individuals either breeding or living in the area during the breeding season (March-August). 191 of these previously identified “resident” individuals were observed during the 2003 wintering season and 161 of them (i.e., marked as chicks) were aged based on their year of ringing. We classified individuals from foreign countries as “wintering immigrants” (N=711): Belgium (12), Denmark (112), France (235), Germany (179), Portugal (106), Switzerland (53), and 14 individuals with unknown (but foreign) band types. Storks with Spanish bands (782) but not encountered during the breeding season were classified as “uncertain”, since an unknown number of resident individuals could have been overlooked during monitoring. Observations of marked storks during the study period at ricefields (coded 1) and dumps (coded 2) or not detected (coded 0) were encoded in individual encounter histories including 80 occasions (days) by group (i.e., 1=certain residents, 2=certain immigrants and 3=uncertain) (Appendix B, Supplement SD1). Age during winter 2003 of known-age residents was incorporated in capture histories as an individual covariate (Appendix B, Supplement SD2).

**Biological hypotheses**—We considered the following biologically plausible hypotheses

(regarding the existence or lack thereof of foraging strategies/preferences and the potential differences between individuals with different traits):

**A. Only generalist individuals:** **1.** *No difference between residents/immigrants and strictly generalist individuals.* The wintering population of storks is composed of generalist individuals that forage at ricefields and dumps in the same proportions (50%). **2.** *No difference between residents/immigrants.* The wintering population of storks is composed only of generalist individuals that forage at ricefields and dumps differentially. **3.** *Foraging habitat use differs between residents/immigrants.* The wintering population of storks is composed only of generalist individuals of which residents and immigrants forage at ricefields and dumps differentially.

**B. Generalists and specialists:** **4.** *No difference between residents/immigrants.* The wintering population of storks is composed of a mixture of ricefield specialists, dump specialists and generalist individuals in the same proportions of residents and immigrants. **5.** *Foraging habitat use differs between residents/immigrants.* The wintering population of storks is composed of a mixture of ricefield specialists, dump specialists and generalist individuals in different proportions of residents and immigrants. Among generalists, residents and immigrants forage at ricefields and dumps differentially.

**C. The role of age:** **6.** *No age effect.* Probabilities of foraging at ricefields by resident storks are similar among age classes. **7.** *Age effect.* Probabilities of foraging at ricefields by resident storks increase with age.

**Multievent capture-recapture models** —*Multievent modelling of foraging strategy and residency status.* We applied a multievent modelling approach (Pradel 2005) able to evaluate the degree of individual consistency in foraging specialisation in relation to residency status

(biological hypotheses 1-5). We present a general multievent model for hypothesis 5 (see below). The alternative hypotheses (1-4) were tested by alternative models fixing or constraining parameters from the general model (Table 1). Models were built and fitted to the data using E-SURGE 1.7.1 software (Choquet et al. 2009b). Model selection was based on the Akaike's Information Criterion (AIC). Additionally, for each model  $j$ , we calculated the Akaike weight,  $w_i$ , as an index of its relative plausibility (Burnham and Anderson 2002).

The multievent framework distinguishes what can be observed in the field (the events coded in the encounter histories) from the underlying biological states of the individuals, which must be inferred (Pradel 2005). Here, the events were '0' (stork not observed on a particular occasion), '1' (stork observed foraging in a ricefield) and '2' (stork observed foraging at a dump). The general model included 7 underlying biological states: 6 states for live resident (R) and immigrant (I) storks belonging to 3 different foraging strategies (see below), coded R1, R2, R3, I1, I2 and I3; and one state for dead individuals, coded D. R1 and I1 represent individuals specialised in ricefields, R2 and I2 represent individuals specialised in dumps, and R3 and I3 represent generalist individuals. Exploratory analyses showed that apparent survival rate during the study period was close to 1 ( $\phi = 0.99999$ ). This is in agreement with the short duration of the study period (80 days) and its timing (winter). Mortality and departure from the study area could therefore be neglected. Thus, we analysed the population as a closed population, allowing an increase in the precision of parameter estimates.

Multievent models use three kinds of parameters: the initial state probabilities, which correspond in our model to the proportions of newly encountered resident/immigrant individuals belonging to the different foraging strategy states (R1, R2, R3, I1, I2 and I3); the probabilities of

transition between the states (i.e., survival probability, which in this case was fixed at 1); and the probabilities of the events, which here involve the probabilities of presence at the two trophic subsidies (ricefields vs. dumps) and resighting probabilities. These parameters were estimated simultaneously from whole encounter histories by maximum likelihood (Choquet et al. 2009b).

Matrix representations with departure states in rows and arrival states in columns are commonly used in multievent models (see a detailed description in Appendix B and pattern matrix in Supplement SP1 and SP2). We broke down the initial state probabilities into two steps: the first step (residency status assignment, matrix 1) corresponded to the probability that a newly encountered individual was a resident “R” ( $\pi$ ) or an immigrant “I” ( $1 - \pi$ ) depending on the group ( $g$ ) in which the individual was previously classified. For the groups with known residency status,  $\pi$  values were fixed at 1 for group 1 (“certain residents”) and at 0 for group 2 (“certain immigrants”). For group 3 (“uncertain”), the proportion of residents was estimated by the model.

$$\text{Residency Status} = \begin{pmatrix} R & I \\ \pi_g & 1 - \pi_g \end{pmatrix} \text{ matrix 1.}$$

The second step corresponded to the individual foraging strategy adopted (matrix 2). The corresponding probabilities denoted by  $\beta$  are conditional on the residency status (R=residents; I=immigrants), thus allowing a differential mixture of foraging strategies at dumps and ricefields between residents (R1, R2 and R3) and immigrants (I1, I2 and I3).

$$\text{Foraging Strategy} = \begin{pmatrix} R1 & R2 & R3 & I1 & I2 & I3 \\ R & \beta_1 & \beta_2 & 1 - \beta_1 - \beta_2 & 0 & 0 & 0 \\ I & 0 & 0 & 0 & \beta_3 & \beta_4 & 1 - \beta_3 - \beta_4 \end{pmatrix} \text{ matrix 2.}$$

The event probabilities were broken down into two steps: the first step corresponded to the daily probabilities of foraging in ricefields ( $\alpha$ ) and dumps ( $1 - \alpha$ ) (matrix 3). They were allowed to

vary with residency status and foraging strategy. In the general model,  $\alpha$  was fixed at 1 for the ricefield specialists (R1, I1), at 0 for dump specialists (R2, I2) and  $\alpha$  was estimated for generalists (R3, I3), representing the daily percentage of generalists foraging in ricefields (Table 1).

$$\text{Foraging} = \begin{matrix} & \begin{matrix} \text{Ricefields} & \text{Dumps} \end{matrix} \\ \begin{matrix} R1 \\ R2 \\ R3 \\ I1 \\ I2 \\ I3 \\ D \end{matrix} & \begin{pmatrix} \alpha_1 & 1-\alpha_1 \\ \alpha_2 & 1-\alpha_2 \\ \alpha_3 & 1-\alpha_3 \\ \alpha_4 & 1-\alpha_3 \\ \alpha_5 & 1-\alpha_5 \\ \alpha_6 & 1-\alpha_6 \\ 1 & 0 \end{pmatrix} \end{matrix} \quad \text{matrix 3.}$$

The second step involved foraging-habitat-specific probabilities of resighting ( $p$ ) (matrix 4). Resighting probabilities in all models were left to vary between ricefields and dumps and over days ( $t$ ) correcting for unbalanced field effort in both habitats (Appendix A). Additionally, we fixed resighting probabilities at 0 in those habitats and days without fieldwork (Appendix A). To avoid overparameterized models we only considered time effects on resighting probabilities.

$$\text{Resighting} = \begin{matrix} & \begin{matrix} 0 & 1 & 2 \end{matrix} \\ \begin{matrix} \text{Ricefields} \\ \text{Dumps} \end{matrix} & \begin{pmatrix} 1-p_{1t} & p_{1t} & 0 \\ 1-p_{2t} & 0 & p_{2t} \end{pmatrix} \end{matrix} \quad \text{matrix 4}$$

Goodness-of-fit tests for multievent models have yet to be developed. The diagnostic goodness-of-fit for the most general model currently available is that of the general Arnason-Schwarz multisite model (Pradel et al. 2005), but this was not appropriate here, as this model, unlike ours, assumes Markovian transitions between sites. Instead, we ran the goodness-of-fit test from the Cormack Jolly Seber model (CJS) assuming full time variation of survival and resighting parameters common to the two types of feeding habitats. We ran this test with U-CARE 2.2.2 software (Choquet et al. 2009a). This test was statistically significant ( $\chi^2 = 627.57$ , d.f.=366,



P<0.001) indicating that individuals tended to be detected on successive occasions (tests 2.CT and 2.CL: trap dependence-like effects, Pradel et al. (2005)). This was expected because of the combination of unequal detectability in the two habitats and the correlation between observations in the ricefields on successive days. Although unequal detectability was treated in our model, the autocorrelation of observations in the ricefields remained untreated. Consequently, we decided to conservatively apply an overdispersion inflation factor (c-hat) of 1.71 calculated as  $627.57/366 (\chi^2/df)$ , which is a reasonable value for a large dataset (Burnham and Anderson 2002).

*Multievent modelling of resident age.* The encounter histories of 161 known-age residents were coded as in the previous analyses and an individual covariate indicating their age at the time of this study (ranging from 3 to 18 years) was included. We developed a simpler multievent model (Appendix B) in which the daily probability of presence at ricefields ( $\alpha$ , matrix 5) was modelled as a linear function of age (hypothesis 7) or as a constant (i.e., no age effects, hypothesis 6).

$$\text{Foraging} = \begin{matrix} & \begin{matrix} \text{Ricefields} & \text{Dumps} \end{matrix} \\ \begin{matrix} R \\ D \end{matrix} & \begin{pmatrix} \alpha & 1-\alpha \\ 1 & 0 \end{pmatrix} \end{matrix} \quad \text{matrix 5}$$

In this analysis no uncertainty in residency status (all individuals were known residents) or different individual foraging strategies were considered. Consequently, individuals belonged to a unique departure state (R) and survival as in the previous model was fixed at 1 (Appendix B). Resighting probabilities were modelled as in the previous modelling approach (matrix 4). The goodness-of-fit of the CJS model was not statistically significant ( $\chi^2=55.89$ , d.f.=70,  $P=0.89$ ) indicating a good fit to the data.

## RESULTS

**Individual patterns of foraging according to residency status**— Overall, 813 storks

(1,332 band readings) were found only at ricefields, 621 individuals (896 readings) only at dumps, and 250 individuals (800 band readings) were observed foraging in both habitats. While this cannot be converted to absolute abundances of birds foraging on each type of food subsidy, it firmly illustrates that the species behaved as a generalist forager. The best-supported model in terms of QAICc was the general model (hypothesis 5, Table 2). Models considering alternative hypotheses showed much larger QAICc values (hypotheses 1-4, Table 2). The selected model (hypothesis 5, Table 2) estimated that 19% (8-40%) of the 782 individuals of uncertain origin would actually be classified as “residents” (n=149), with the remaining uncertain individuals classified as “immigrants” (n=633). This leads to mean estimates of 340 (i.e., 191+149) resident and 1,344 (i.e., 711+633) immigrant marked storks wintering in the study area.

Resident individuals showed a high consistency in their choice of food subsidies: 72% (CI: 60-81%) of residents daily foraged exclusively in ricefields (i.e., were ricefield specialists, n=245 individuals), while the remaining individuals (28%, CI: 19-40%, n=95 individuals) behaved as generalists. Among resident generalists using both foraging habitats during the study period, 31% (CI: 18-49%) and 69% (CI: 51-82 %) of individuals daily foraged in ricefields and dumps, respectively. Dump specialisation did not occur among residents as the proportion of dump specialists (R2 foraging strategy) was 0. In contrast, immigrants exhibited the three different foraging strategies: 16% (CI: 9-18%) were ricefield specialists (n=215 individuals), 24% (19-31%) were dump specialists (n=323 individuals) and 60% (CI: 50-68%) were generalists (n=805 individuals). 60% (CI: 52-67%) and 40% (CI: 33-0.48%) of immigrant generalists daily foraged in ricefields and dumps, respectively. Consequently, on a daily basis, 81% of resident and 52% of immigrant storks foraged in ricefields. These proportions lead to estimates of 710 marked storks

daily foraging in dumps (65 residents and 645 immigrants) and 974 marked storks daily foraging in ricefields (275 residents and 699 immigrants).

**The effect of age as a driver of individual specialisation**— Resident storks showed higher probabilities of foraging in ricefields with age (Fig 2). Accordingly, the model considering an individual age effect on probabilities of foraging in ricefields was better supported in terms of AICc than the model without age effects (hypothesis 7 vs. hypothesis 6, Table 2). The effect of age was statistically significant, as confidence intervals of the beta estimate corresponding to the linear slope did not include zero (1.32, CI: 0.38-2.27).

**Spatial foraging patterns**— For individuals seen in at least two localities, the distance between the farthest pair of localities was slightly longer for immigrants than for resident individuals (average, range): 22.8, 3.5-116.0 Km, and 17.8, 3.5-72.2 Km, respectively (Mann-Whitney  $W = 6833$ ,  $p = 0.09$ ). This was due to the fact that distances between dumps (highly used by immigrants) were higher than distances between ricefields (Fig. 1). However, both immigrants and residents moved throughout the study area (Fig. 1).

## DISCUSSION

### Individual traits as drivers of foraging specialisation

The existence of intraspecific differentiation in niche or personality has received special attention during the last decade (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012). Less is known, however, about the ecological causes of individual specialisation (Araújo et al. 2011) or its long-term evolutionary consequences (Dall et al. 2012). Here, we studied the role of individual traits (residence status and age) on foraging specialisation under the optimal foraging theory framework (Araújo et al. 2011). We found that at the population level wintering white storks in SW Spain

used two anthropogenic food subsidies in large numbers as would be expected in an opportunistic generalist species. However, individual storks were either specialists or generalists on their foraging substrates (ricefields or dumps) during the study period (autumn-winter 2003). Although our study reflects a specialisation on a particular foraging habitat type rather than on a specific diet (i.e. prey items), crayfishes are the prey most frequently consumed by wintering white storks in ricefields (ranging from 86% to 98 % in two different winters, Tablado et al. 2010). On the contrary, storks can forage on a large variety of refuse items at dumps of likely lower nutritional quality than that of crayfish, a prey very rich in carotenoids (Negro et al. 2000).

As predicted, residents were highly specialised in feeding at ricefields, with no residents specialised in feeding at dumps. On the contrary, we found a slightly higher proportion of immigrants specialising in dumps than in ricefields, but most immigrant individuals (60%) were generalists. Moreover, diet preferences changed with age. According to our prediction, older resident storks had a higher probability of foraging in ricefields than younger individuals, suggesting that foraging skills in this particular habitat may increase with age and thus with accumulated learning and experience in the area (Marchetti and Price 1989, Giraldeau and Caraco 2000). Wintering immigrants were similarly specialised on dumps and ricefields. High annual fidelity to wintering areas observed in other long-lived birds (Sanz-Aguilar et al. 2012) could explain the ricefield specialisation of some wintering immigrant individuals (as in residents) through the acquisition of experience in the area. On the other hand, supplementary feeding programs carried out in several European countries for the conservation of the species may have habituated certain individuals to highly predictable food resources such as dumps (Doligez et al. 2004, Schaub et al. 2004, Massemin-Challet et al. 2006). A non-exclusive alternative hypothesis

would be that specialisation on dumps may only occur among juvenile immigrants. Note that resident juvenile storks (younger than three years old) were not present in our sample. In fact, all 42 satellite-tracked juveniles born in the study area wintered in African quarters during their first years of life (J. Blas, unpubl. data). This could also explain the lack of dump specialisation among residents. Unfortunately, we have no data on the previous experience of immigrant storks wintering in the study area to test this hypothesis.

### **Ecological implications and consequences of foraging specialisation**

At the individual level, two studies on seabirds related the existence of individual foraging specialisation on anthropogenic food subsidies with long-term fitness consequences: Northern gannets, *Morus bassanus*, foraging on fisheries discards and Western gulls foraging on refuse showed a lower body condition and lifetime reproductive success, respectively, than individuals actively preying upon live fish (Annett and Pierotti 1999, Votier et al. 2010). In our study case, an alternative but non-exclusive hypothesis to explain the age-related increased probability of foraging in ricefields would be differential survival (Curio 1983, Marchetti and Price 1989); i.e., if individuals consistently foraging in ricefields survive more, they would be overrepresented among older age classes. However, since our study only covered one wintering season, further research on long-term consistency of individual foraging specialisation and its potential demographic and population effects is needed.

At the population level, the high availability of food resources at rubbish dumps throughout the wintering and along the breeding range of white storks has promoted behavioural, demographic and population changes in this (Tortosa et al. 1995, 2002, Doligez et al. 2004, Schaub et al. 2005, Massemin-Challet et al. 2006) and other animal species (Oro et al. 2013).



Moreover, selection processes (e.g., wintering mortality or nest failure) have been relaxed by shortened migratory distances and greatly increased food availability (Tortosa et al. 2002, Schaub et al. 2004). Our study model demonstrates the existence of both consistent (i.e., specialist) and flexible (i.e., generalist) individual foraging strategies among the wintering population of white storks in the Doñana marshlands. The existence of consistent individual behaviours has been recognized as a driver of adaptation to new environments (i.e., new anthropogenic niches, Carrete and Tella 2011, 2013). Moreover, individual experience (shaped by age and origin) seems to be the most plausible mechanism responsible for differential use of subsidies. This has implications for our understanding of how a population-level generalist species such as the white stork could cope with anthropogenic habitat changes (Oro et al., 2013).

Doñana marshlands represent the most important European wintering area for the species and numbers of immigrant storks largely exceed the number of residents. Although ricefields were preferentially selected by resident storks, many individuals foraged daily at dumps; mainly immigrants (48%) and young residents (Fig. 2). Storks at Doñana benefited from two anthropogenic subsidies, but crayfishes are not available in other wintering areas. European environmental policies are now directed at curtailing food accessibility (i.e., biodegradable waste) to animals in rubbish dumps by 2016 (Directive 2001/77/EC), and an effect on wintering white storks is expected (<http://www.bto.org/science/migration/tracking-studies/stork-tracking>). Although white stork populations have grown spectacularly during the last two decades after becoming endangered in the 1950-60's, several populations remain small (Thomsen and Hötter 2006).

Our results predict interesting consequences of potential dump management. Future food

limitations may have important consequences at the population level (Oro et al. 2013), with wintering migrant storks from northern European populations being potentially more affected due to the large number of wintering birds and their greater use of dumps. While dump closure could appear to be a local phenomenon, our results suggest that it would directly affect stork populations thousands of kilometres away (immigrant storks), rather than just the local population (Peters et al. 2007). However, immigrant storks were highly generalist at the individual level. Thus, an eventual dump closure would increase the number of immigrant storks feeding on ricefields, increasing competition and reducing resource availability for the resident population.

#### **Methodological aspects and opportunities of multievent models**

Repeated observations over time in individual foraging choices are essential to correctly study and quantify the consistency of individual foraging specialisation (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012). However, perfect detection of individuals in natural conditions is often rare or costly. Here, we developed for the first time a capture-recapture modelling approach to calculate consistency in individual behaviour using capture-recapture data. This new method allowed a robust quantification (including confidence intervals) of individual strategies with the incorporation of imperfect detection of individuals. Additionally, we extended our modelling approach to allow uncertainty in individual classification (which in other cases may correspond to sex, breeding status or other factors, Pradel 2005, Frederiksen et al. 2013; see in particular Gourlay-Larour et al. (2014) for another study separating immigrants from residents on a wintering ground). In this way, we were able to estimate the proportion of resident individuals missed despite intense breeding monitoring, a parameter currently impossible to derive with other methods. Our model assumes that observations of the same individual on different dates are

uncorrelated and that individuals move independently of each other. This is probably not true as individuals may preferentially return to a site where they were able to forage successfully and individuals may also use the behaviour of conspecifics as clues to find suitable sites. These types of dependency and any remaining heterogeneity among individuals beyond the factors incorporated in our model (foraging strategy and residency status) are why goodness-of-fit tests were significant. When such non-structural departures are involved, the use of a variance inflation factor protects against the detection of spurious effects at the expense of power (Burnham and Anderson 2000). This is the approach we adopted. Moreover, our large numbers of individuals with certain residency status allowed us to repeat the analyses without the individuals of uncertain residency status with similar results, demonstrating the robustness of our multievent approach, which deals well with uncertainty (Appendix B). The use of this approach is therefore useful when sample sizes are logistically constrained and the proportion of individuals of uncertain status/behaviours is necessarily large. A step-by-step description of the analyses is provided in the supporting information with the aim of encouraging the application of our multievent model to other studies.

This study emphasised the application of longitudinal data on replicated observations of individual resource use over time for quantitative studies on individual foraging specialisation (Araújo et al. 2011). Tracking technologies are becoming very valuable tools to monitor individuals over large temporal and spatial scales (Millsbaugh and Marzluff 2001), including European storks (<http://projekt-storchenzug.com/>). However, sample size is usually small due to high costs. In contrast, extensive marking programs, such as those carried out with European white storks, allowed the identification and monitoring of a large number of individuals. Capture-

recapture methods were developed to estimate demographic parameters while accounting for imperfect detection of individuals. Today, the flexibility of multistate and recently of multievent models, as presented here, has allowed the study of additional parameters of interest (Clutton-Brock and Sheldon 2010, Frederiksen et al. 2013) and the incorporation of discrete individual heterogeneity classes (i.e., finite-mixture models) in capture-recapture modelling (Pledger 2000, Pradel 2005). Our study provides a robust new modelling approach for the study of individual behavioural specialisation from non-invasive and imperfect individual resightings in the wild. Further studies could also consider the potential dependence among individual decisions as white storks usually gather at foraging sites forming large groups, both in our study area and in other populations (e.g., Carrascal et al. 1990, Giraldeau and Caraco 2000). However, models including dependence among individuals forming groups have only been developed for fixed groups (with individuals belonging to the same group during the whole study period, Choquet et al. 2013), and further research is needed to determine the consistency of membership composition of foraging groups in white storks. Nonetheless, survival parameters have been found to be robust when dependence in recapture among individuals occurs (Choquet et al. 2013).

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- 598
- 599 Appendix A. Field work details.
- 600 Appendix B. Multievent analyses details.
- 601 Supplement SD1. Dataset: capture histories of all resident, immigrant and uncertain storks.
- 602 Supplement SD2. Dataset: capture histories of resident known-age storks.
- 603 Supplement SP1. Pattern files for the general model.
- 604 Supplement SP2. Pattern files for the simplified model for known-age residents.

**Table 1.** Multievent model constraints. Parameters fixed and/or constrained to be equal (=) or different ( $\neq$ ). Notation:  $\pi$  is the probability that a newly encountered individual is a resident;  $\beta$  is the probability of adopting a foraging strategy by resident storks type 1 and 2 ( $\beta_1, \beta_2$ ) and immigrant storks type 1 and 2 ( $\beta_3, \beta_4$ );  $\alpha$  is the probability of foraging in ricefields of resident storks type 1, 2 and 3 ( $\alpha_1, \alpha_2, \alpha_3$ ) and immigrant storks type 1, 2 and 3 ( $\alpha_4, \alpha_5, \alpha_6$ ); group 1 and 2 correspond to storks recognized as residents and European immigrants, respectively.

Model	Initial State step 1	Initial State step 2	Event, step 1
Hypothesis 1	$\pi = 0$	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$(\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha_5 = \alpha_6) = 0.5$
Hypothesis 2	$\pi = 0$	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha_5 = \alpha_6$
Hypothesis 3	$\pi$ (group 1) = 1 $\pi$ (group 2) = 0	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$(\alpha_1 = \alpha_2 = \alpha_3) \neq (\alpha_4 = \alpha_5 = \alpha_6)$
Hypothesis 4	$\pi = 0$	$\beta_1 = \beta_3 \neq \beta_2 = \beta_4$	$(\alpha_1 = \alpha_4) = 1$ $(\alpha_2 = \alpha_5) = 0$ $(\alpha_3 \neq \alpha_6)$
Hypothesis 5	$\pi$ (group 1) = 1 $\pi$ (group 2) = 0	$\beta_1 \neq \beta_2 \neq \beta_3 \neq \beta_4$	$(\alpha_1 = \alpha_4) = 1$ $(\alpha_2 = \alpha_5) = 0$ $(\alpha_3 \neq \alpha_6)$



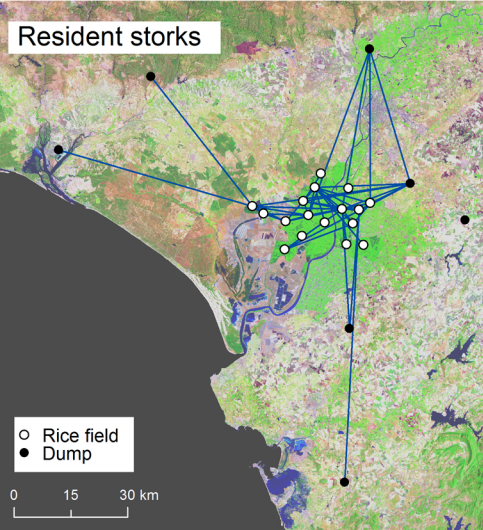
**Table 2.** Multievent capture-recapture modelling of white stork probabilities of foraging in ricefields and dumps testing the effects of residency status and foraging strategy (Hypotheses 1-5) and individual age (Hypotheses 6-7). Notation, np: number of estimable parameters; QAICc: Akaike information criterion corrected for overdispersion and small sample size;  $\Delta$ QAICc: the QAICc difference between the current model and the one with the lowest QAICc value;  $w_i$ : Akaike's weight.

Model	np	Deviance	QAICc	$\Delta$ QAICc	$w_i$
Hypothesis 1	74	14440.52	8596.51	258.13	0
Hypothesis 2	75	14402.66	8576.47	238.10	0
Hypothesis 3	78	14262.36	8500.74	162.36	0
Hypothesis 4	78	14051.93	8377.68	39.31	0
Hypothesis 5	82	13970.27	8338.37	0	1
Hypothesis 6	65	1127.96	1278.12	5.87	0.05
Hypothesis 7	66	1119.42	1272.25	0	0.95

**Figure 1.** Study area in SW Spain (inset map, orange square and arrow) showing all localities where white storks were observed foraging in dumps and ricefields (white and black dots). Lines link pairs of localities sharing at least one individual stork.

**Figure 2.** Probability of resident storks foraging in ricefields rather than in dumps during the 2003 wintering season in southern Spain (solid line) and CI (dashed line) related to individual age.

Resident storks



Immigrant storks

